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Estimated size of the Northwest Atlantic grey seal population 1977-2010

Évaluation de la population de phoques gris de l'Atlantique Nord-Ouest, 1977-2010

L. Thomas[1], M.O. Hammill[2], and W.D. Bowen[3]

[1]Centre for Research into Ecological and Environmental Modelling, University of St Andrews St Andrews, Fife KY16 9LZ. Scotland.

[2]Maurice Lamontagne Institute, Dept of Fisheries and Oceans P.O. Box 1000, Mont Joli QC. G5H 3Z4. Canada.

[3]Population Ecology Division, Bedford Institute of Oceanography, Dept of Fisheries and Oceans Dartmouth NS. B2Y 4A2. Canada.

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ABSTRACT

We constructed a stochastic model of Northwest Atlantic grey seal population dynamics and fit it to available pup production data from 1977-2010 divided into three breeding regions: Sable Island, Gulf of St. Lawrence, and Coastal Nova Scotia (including Hay Island and other small colonies along the coast of Nova Scotia). The model and fitting methods are the same as those used in a previous population assessment (Thomas et al. 2007), updated with 2010 pup production data and revised estimates of historical harvest. The model assumes that fecundity rates are age-dependent but are constant over time, that adult survival rates are constant, and that pup survival is density dependent. Females are assumed to be able to move to a new region to breed if pup survival is higher there, but once they start breeding they do not move. We used a Bayesian computer-intensive method (particle filtering) to fit the model, with informative priors on model parameters.

The posterior estimates for some parameters were close to their priors, indicating little information about these parameters in the pup production data and highlighting the importance of carefully choosing the priors. Other parameters were far from the prior: in particular the posterior estimates of carrying capacity were far higher than the prior values, indicating little evidence of density dependent population regulation at current levels of pup production. The total estimated population size at the end of the 2010 breeding season (i.e., including pups) was 348,900 (95% CI 291,300-414,900). This is 4% higher than the equivalent estimate for 2009 of 335,200 (95%CI 292,000-395,100) and 975% higher than the estimate for 1977 of 35,800 (95%CI 24,700-53,100). Average annual rates of population increase are estimated to be 6% in the 1980s, 9% in the 1990s and 6% in the 2000s. These estimates should be treated with some caution because: (1) the biological model showed clear lack of fit, particularly to the Gulf data where extending the model to account for ice and weather conditions would be useful; (2) sensitivity of the results to the priors used has not been assessed; and (3) the fitting algorithm may have caused some (small) biases.

RÉSUMÉ

Nous avons élaboré un modèle stochastique de la dynamique de la population de phoques gris de l'Atlantique Nord-Ouest et y avons intégré les données existantes de production des jeunes phoques de 1977 à 2010, issues de trois aires de reproduction : l'île de Sable, le golfe du Saint-Laurent et la côte est (y compris la colonie de l'île Hay et d'autres petites colonies situées le long de la plateforme Néo-Écossaise). Le modèle et les méthodes d'ajustement sont les mêmes que ceux utilisés dans une évaluation précédente de la population (Thomas et al. 2007), mis à jour avec les données de la production de petits phoques de 2010 et les prévisions révisées de la récolte historique. Le modèle permet de supposer que les taux de fécondité dépendent de l'âge, mais qu'ils demeurent néanmoins constants dans le temps, que les chances de survie des petits phoques sont liées à la densité, que les femelles sont capables de se déplacer vers une autre région pour se reproduire si les chances de survie des bébés phoques y sont plus élevées, mais qu'une fois fécondées, elles ne bougent plus. Nous avons employé une méthode bayésienne reposant largement sur le traitement informatique (filtrage de particules) pour l'adaptation d'information a priori sur les paramètres du modèle.

Les estimations postérieures de certains paramètres se sont montrées relativement proches des données a priori, révélant l'existence de très peu d'information sur ces paramètres dans les données sur la production des bébés phoques et faisant ressortir l'importance de bien choisir les éléments a priori. Par contre, d'autres paramètres étaient très éloignés de l'information a priori, surtout dans le cas des évaluations postérieures de la capacité de charge, qui étaient beaucoup plus élevées que les valeurs a priori, montrant très peu de signes d'une dépendance de la régulation de la population à l'égard de la densité, au taux actuel de production des petits. En 2010, l'estimation de la population (comprenant les petits) au terme de la saison de reproduction était de 348 900 (IC de 95 % = 291 300-414 900). Cela représente une hausse de 4 % par rapport à l'estimation comparable de 2009 qui totalisait 335 200 (IC de 95 % = 292 000-395 100) et de 975 % comparativement à celle de 1977 qui était de 35 800 (IC de 95 % = 24 700-53 100). Au cours des années 1980, la progression annuelle de la population était évaluée à 6 %, à 9 % durant les années 1990 et à 6 % pendant les années 2000. Il importe toutefois d'user de prudence dans la mention de ces estimations puisque : 1) le modèle biologique a révélé une très faible corrélation, surtout en ce qui concerne les données du Golfe où il serait utile d'élargir la capacité du modèle de manière à tenir compte de l'état des glaces et des conditions météorologiques, 2) la sensibilité des résultats aux valeurs a priori n'a pas été évaluée et 3) l'algorithme employé est susceptible d'avoir introduit certaines erreurs.

INTRODUCTION

The aim of this paper is to present preliminary estimates of population size for the Northwest Atlantic grey seal (*Halichoerus grypus*) for the period 1977-2010, updating estimates from a previous assessment (Thomas et al. 2007) in the light of new survey data and slightly revised estimates of historical harvest levels.

Seals (and marine mammals in general) are notoriously difficult to census: they spend much of their time at sea and most of that underwater. The only time a substantial part of the population is in one place is during the breeding season, when pre-weaned pups are readily counted on breeding colonies, and for this reason pup production estimates form the principal tool for population monitoring.

The breeding population of Northwest Atlantic grey seals is normally divided into two components for management purposes, based on the locations of the largest breeding colonies. These are the Sable Island component and traditionally a Gulf of St. Lawrence (Gulf) component (Mansfield and Beck 1977). However, recent changes in the distribution of pupping warrant following Thomas et al. (2007) by dividing the population into three parts ("regions"), for the purposes of modelling: Sable Island, Gulf and Coastal Nova Scotia (Fig. 1). Pup production on Sable Island has been relatively well monitored, with pup production estimated in most years from 1962 to 1990 by tagging all weaned pups (Mansfield and Beck 1977, Stobo and Zwanenburg 1990) and more recently at longer intervals via aerial photography (Bowen et al. 2007). The Gulf region comprises animals that whelp primarily on the drifting pack ice in Northumberland Strait and those born on small islands located within the southern Gulf of St. Lawrence. Pup production here has been estimated approximately every 4 years from mark-recapture studies (Hammill et al. 1992, 1998, Myers et al. 1997) and aerial surveys (Hammill and Stenson 2011). The estimates have higher standard errors (SEs) than those from Sable Island because of more difficult conditions in this area (Myers et al. 1997, Hammill et al. 1998). The third region, the Coastal Nova Scotia, is by far the smallest part of the population. It comprises seals that whelp primarily on Hay Island, but also includes some other small islands along the coast of Nova Scotia. These have been monitored intermittently by visual counts or year-class tagging (Hammill et al. 2007). All three regions were surveyed most recently in spring 2010 (Bowen et al. 2011). The pup production data used here are shown in Appendix Table A1.

To estimate total population size from pup production data, it is necessary to make assumptions about the relationship between pup production and numbers of seals in other age classes, and between observed and actual pup production. We do this using a stochastic discrete-time modelling framework called a state-space model. The use of this framework to describe and fit models of wildlife population dynamics is described by Buckland et al. (2004), and examples of its application to the British population of grey seals are given by Thomas et al. (2005), Newman et al. (2006), Buckland et al. (2007) and Newman et al. (2009). The model used here has previously been used to estimate Northwest Atlantic grey seal population size in 2007 (Thomas et al. 2007), and similar models have been used by the UK Special Committee on Seals for grey seal population assessment since 2003 (Thomas and Harwood 2003, 2004a, b, 2005, 2006, 2007, 2008, 2009; Thomas 2010).

Following Trzcinski et al. (2006), we consider population dynamics models that allow for density dependent declines in vital rates in response to increases in population size. Analysis of pregnancy rates from adult females taken as part of a scientific sampling program between 1969 and 2007 showed age but not time-specific variation in pregnancy (Thomas et al. 2007), and we therefore assume here that fecundity rates vary by age, but not over time. The model

does, however, allow for a density dependent decline in pup survival, with carrying capacity of pups in each region being a model parameter.

Specifying complex models for wildlife population dynamics is relatively simple, but fitting them to observed data is often not so straightforward (Buckland et al. 2007, Newman et al. 2009). We employ a computer-intensive Bayesian fitting method called Monte Carlo particle filtering (also called sequential importance sampling), identical to that used by Thomas et al. (2007). A particle filter is an algorithm that produces a set of weighted samples (particles) taken from the prior distributions on the parameters and states (seal numbers) and projected forward stochastically through the time series. The weights relate to the manner in which the particles were sampled, how they were projected forward and the likelihood of the observed pup production given the simulated pup numbers. An accessible tutorial in the context of state-space models for wildlife population dynamics is given by Newman et al. (2006), and applications using particle filters are given by Thomas et al. (2005), Thomas and Harwood (2003, 2004a, b, 2005, 2006, 2007, 2008, 2009) and Thomas (2010). A general comparison between particle filtering and other fitting methods, such as Markov chain Monte Carlo (MCMC) in this context is given by Buckland et al. (2007), and a detailed comparison using a state-space model for British Grey seals applied to real and simulated data is given by Newman et al. (2009).

Bayesian methods require prior distributions to be specified for all random quantities. We use informative prior distributions on model parameters, such as survival rates, fecundity rates and movement parameters. These are mostly taken from expert opinion, but our prior on fecundity rates comes from the analysis of pregnancy rates undertaken by Thomas et al. (2007).

MATERIALS AND METHODS

STATE-SPACE MODEL

A state-space model has two components: (1) the state process, which models the true but unknown state of the population (in this case numbers of seals of different ages in different regions); and (2) the observation process, which models how the survey data are generated given the true states.

We divided the seal population in each breeding region into 7 age classes: pups (age 0, and also sometimes referred to as "young-of-the-year" or YOY), age 1 to 5 adult females, and age 6 and older females. Note that our model does not explicitly include adult males – see below for assumptions required to calculate male population numbers.

The time step for the process model is 1 year, beginning just after the breeding season. The model is made up of 5 sub-processes: harvest, survival, ageing, movement of age 3 females, and breeding.

Harvest consists of removal of what are assumed to be known numbers of animals in each region, killed as a result of the commercial hunt, culls, removal of nuisance animals, and scientific sampling. Cull and commercial harvest data were divided into YOY (age 0 animals) and adults (animals aged 1 and older). Within the adult age group, the numbers of each age and sex removed from the population were assumed to be in proportion to their relative frequency in the population. For example, if 75 adults were known to have been removed from a particular region in a particular year, and there were estimated to be 100, 80, 60, 50, 40 and 120 female seals of ages 1 through to 6+ respectively with an equal adult sex ratio, then we

assumed that 8, 7, 5, 4, 3 and 10 females were removed from each age class, respectively. For removal of nuisance animals and scientific sampling, data was only available pooled across YOY and adult age categories, so we assumed that removal was in proportion to age and sex frequencies in the population, including YOY (which includes both male and female pups). Note that the above method of dealing with harvest data is slightly different from that of Thomas et al. (2007), where three age categories of data were used, and that the historical harvest data has been updated since that report, so that slightly different numbers were used. The values used are given in Appendix Table A2.

Survival is modelled as a binomial random process, and is assumed additive to harvest (i.e., occurring after numbers removed by harvest). We assume that pup survival is density dependent, and follows a Beverton-Holt function of the form:

$$\phi_{p,r,t} = \frac{\phi_{p\max}}{1+\beta_r n_{0,r,t-1}} \qquad (1)$$

where $n_{0,r,t-1}$ is the number of pups born in region r in year t-1, $\phi_{p,r,t}$ is survival rate of these pups, $\phi_{p\max}$ is maximum pup survival rate, and β_r is inversely proportional to the carrying capacity of the region ($\beta \geq 0$). We assume that half of the pups born will be male; hence the expected number of female pups surviving will be $0.5\phi_{p,r,t}n_{0,r,t-1}$. We assume that adult female survival rate, ϕ_a is constant across regions and time.

Ageing is deterministic – all seals age by one year (although those in the age 6+ category remain there).

To model movement, we assume that only females age 3 (i.e., before breeding age) may move from their natal region, and thereafter females remain in the region they are in. We assume that movement is fitness dependent, such that females will only move if the expected survival of their future offspring is higher elsewhere, and the probability of movement is proportional to the expected survival difference. We measure the propensity for fitness-dependent movement relative to a competing propensity for site fidelity, which means that many females will not move even if conditions for their pups would be better elsewhere. We assume that numbers in each region after movement is a multinomial random variable:

$$\left(n_{3,1,t}, n_{3,2,t}, n_{3,3,t}\right) \sim Multinomial\left(\sum_{r=1}^{3} n^{*}_{3,r,t}, p_{1,t}, p_{2,t}, p_{3,t}\right) \qquad (2)$$

where $n^{*}_{3,r,t}$ and $n_{3,r,t}$ denote numbers of age 3 females in region r before and after movement respectively, and $p_{r,t}$ is the probability that a seal aged 3 is in region r after movement. We model this probability as

$$p_{r,t} = \frac{\sum_{j=1}^{3} n^{*}_{3,j,t}\delta_{j\to r,t}}{\sum_{j=1}^{3} n^{*}_{3,j,t}} \qquad (3)$$

where

$$\delta_{j\to r,t} = \frac{I[j=r] + \gamma \max\left(\phi_{p,r,t} - \phi_{p,j,t}, 0\right) I[j \neq r]}{1+\gamma \max\left(\phi_{p,r,t} - \phi_{p,j,t}, 0\right)} \qquad (4)$$

with $I[.]$ being an indicator function that takes value 0 if the condition inside the bracket is met and zero otherwise, and γ being a parameter regulating the strength of density-dependent movement versus site fidelity (the larger γ, the stronger the effect of density dependence;

$\gamma \geq 0$). This movement model is a simpler version of that used by Newman et al. (2009), which had an additional parameter to make movement less likely among more widely spaced regions.

We model breeding by assuming that the number of pups produced is a binomial random variable, with a fecundity rate that is age but not time dependent. We assume that females age 3 or less at the time of the breeding season do not breed, while fecundity rate for females of age 6+ at the time of the breeding season is governed by a model parameter $\alpha_{\max}$. For females age 4 and 5, fecundity rates are given by

$$\alpha_a = \alpha_{\max} \log it^{-1}(\rho(a-4.5)) \quad (5)$$

where ρ is a model parameter that determines how fecundity rate increases with age ($0 \leq \rho < 1$) towards $\alpha_{\max}$.

For the observation process, we assume that pup production estimates follow a normal distribution, with known standard error.

In summary, there are 8 model parameters: adult survival ϕ_a, maximum pup survival $\phi_{p\max}$, one carrying capacity parameter-related parameter for each region $\beta_1 - \beta_3$, a parameter regulating movement rates γ, maximum fecundity $\alpha_{\max}$, and a parameter regulating increase in fecundity with age, ρ.

DATA AND PRIORS

The input data were pup production estimates for 1977-2010, together with their estimated standard errors (SEs, Appendix Table A1). In some cases the estimates are weighted means of independent estimates in each year; in other cases the SEs are assumed – see Thomas et al. (2007) for details. To allow the fitting algorithm to produce reliable results in the time available to run it, the SEs in Table A1 were multiplied by 3 in the analyses reported here (see *Discussion*).

Cull and commercial harvest data were segregated into young-of-the-year (age 0) and adults (ages 1+) as described previously; nuisance and scientific removal data were un-segregated (Figure 2 and Appendix Table A2).

Prior parameter estimates are given in Table 1. Priors on fecundity rates come from the analysis of pregnancy rate data (Thomas et al. 2007). Priors on other parameters came from previously published papers, supplemented by expert opinion.

We followed Thomas and Harwood (2005, and later reports by the same authors) in using a re-parameterization to specify the prior on the β_rs in terms of a prior on the pup production at carrying capacity, χ_r, conditional on the values of the other model parameters. For the model outlined above, it can be shown that expected pup survival rate at equilibrium, ϕ_p^*, is given by

$$\phi_p^* = \frac{1}{0.5\phi_a^3\left(\alpha_4 + \phi_a\alpha_5 + \frac{\phi_a^2\alpha_{6+}}{1-\sigma_a}\right)} \quad (6)$$

Substituting (6) into (1) and re-arranging, we find that for a given carrying capacity of pup production at equilibrium, χ_r,

$$\beta_r = \frac{1}{\chi_r}\left(\phi_{p\max} 0.5\phi_a^3\left(\alpha_4 + \phi_a\alpha_5 + \frac{\phi_a^2\alpha_{6+}}{1-\sigma_a}\right) - 1\right) \quad (7)$$

The priors on carrying capacity of pups at equilibrium were set by specifying a prior mean of approximately twice the largest observed count in each region, with a large prior variance (equivalent to CV of 50%) to reflect the uncertainty in specifying these values a priori. (In cases where the largest count came from the 2010 surveys, the prior was kept the same as that used by Thomas et al. (2007) for comparability.)

The prior mean on the movement parameter was specified by calculating the value that would lead to a 10% emigration of age 3 seals from a region to one where pup survival was 0.1 higher. This value (2.5) was also given a large variance (equivalent to a CV of 100%) to reflect the arbitrary nature with which it was chosen.

Prior distributions are also required on seal population size by age and region for the first year (1977); the Markovian nature of the model means that prior distributions on population size for other years are defined automatically after specifying those in the first year and the parameters.

We based our method of specifying priors on the population size in the first year on that of Thomas et al. (2005). This method uses the first year of data to specify a prior distribution on pup numbers in each region, and then uses this distribution together with the demographic parameters to derive priors for the other age classes (see Thomas et al. 2005 for details). Pup production estimates were not available in 1977 for the Coastal Nova Scotia region, so the estimate for 1976 was used in its place.

FITTING METHOD

The particle filtering algorithm we used is similar to that described by Thomas and Harwood (2007) and Newman et al. (2007), implemented in the C programming language. An outline of the main features of the algorithm is given below, for completeness – it is not necessary to read the rest of this sub-section to understand the results that follow. For reference, we highlight any differences from the Thomas and Harwood (2007) algorithm. The algorithm is identical to that used by Thomas et al. (2007).

Initial rejection control. The aim of this procedure is to weed out at an early stage sets of parameter and state combinations that are simulated from the prior but clearly have very low density in the posterior, so that computer time can be focussed on areas of parameter and state space that have higher posterior density. We simulated sets of 1,000,000 particles from the prior distributions, projected them forwards from 1977 to 1978 and calculated likelihood weights based on the 1978 data. We then applied rejection control, an algorithm that probabilistically removes particles with low weight (Liu 2001), using the mean of the particles weights as the rejection control criterion. This typically resulted in about a quarter of the particles being retained. We repeated this process until we had at least 1,000,000 particles surviving the initial rejection control stage.

Auxiliary particle filter (Liu and West 2001). With this procedure, we projected forward one time step at a time, starting in 1978, initially deterministically. We then resampled the particles using the deterministic weights – i.e., according to the expected pup production in the next time period – thereby producing a set of "promising" particles. Because data for the Gulf and Coastal Nova

Scotia regions were missing in many years, it seemed prudent not to follow the usual convention of resampling with probability proportional to the weights. Instead, we used the more conservative strategy (Liu 2001) of resampling with probability proportional to the square root of the weights (this is one point of difference from the Thomas and Harwood (2007) algorithm). Resampled copies of the same ancestor particle will have the same parameter values, so to maintain parameter diversity we used kernel smoothing to jitter the parameter values (see Liu and West 2001 for details). This can cause bias, so we kept the amount of kernel smoothing to a minimum, using a discount value of 0.9997 (a value of 1.0 results in no jittering at all; a value of 0.997 was used by Thomas and Harwood (2007)). After kernel smoothing, particles were then projected forward stochastically to the next time period, and weights were adjusted to take account of the initial resampling. The auxiliary particle filter was not used in years where there was no data in any region – in this case particles simply projected forward stochastically, without any re-weighting or resampling.

Final rejection control. At the last time period, rejection control was used to reduce the number of particles that must be stored. The rejection control criterion was the mean of the particle weights. This reduced the number of particles stored per run from 1,000,000 to between 600,000 and 700,000.

Multiple runs. The above procedures generated samples based on 1,000,000 particles (although fewer were stored after the final rejection control). However, even this many samples gave a very imprecise estimate of the posterior distributions of interest for all models. Hence, many multiple runs (100 or more) were required to reduce Monte Carlo error to acceptable levels. To reduce the resulting outputs down to a manageable level for post-processing (i.e., calculating posterior distributions on quantities of interest), it was necessary to apply further rejection control, this time using a rejection control criterion of the 99.999^{th} percentile of the particle weights from all of the multiple runs for a particular model.

One last difference between the algorithm of Thomas and Harwood (2007) and that used here was that the former used an analytic integration procedure to enable efficient estimation of an observation error parameter; here the observation SEs were assumed known.

ESTIMATING TOTAL POPULATION SIZE

Our state-space model does not include adult males. Nevertheless, if we follow Hammill and Gosselin (2005) and Trzcinski et al. (2006) in assuming male and female survival rates are the same, then total population size can be estimated as twice the adult female population size plus the estimated pup production. We take this approach in giving total population size estimates by region and year, and summed over regions. We also use the estimated male numbers to divide the harvest of adults by sex. This same assumption was used by Thomas et al. (2007).

RESULTS

STATE-SPACE MODEL

The results reported here are based on 150 runs of 1 million particles. This represents approximately 60 hours of computer time, although in practice runs were made in parallel on up to 8 processors so results were available in less than 2 days. After the final rejection control step of the particle filtering algorithm, 3.0 million particles remained.

Since the resampling step of the auxiliary particle filter makes multiple copies of the same particles, the surviving particles are no longer independent, so the true sample size of independent particles is much lower than total sample size. A useful approximate index of whether there have been enough runs for Monte-Carlo error to be acceptably low is the total number of unique ancestral particles (i.e., independent samples from the prior) surviving in the final results, weighted by the particle weights to produce an "effective" sample size of unique ancestral particles, ESS_u (Thomas 2010). Thomas (2009) found that for UK grey seals, population estimates were accurate to 2-3 significant figures with ESS_u values of 500 or less; here the ESS_u was 920.8 so results are expected have greater accuracy than that.

Estimated pup production[1] for the three regions is shown in Figure 3, and values are given in Appendix Table A3. The estimated trajectory for the Sable region fits the data quite well. The trajectory appears near-exponential, but there is some evidence that the rate of population increase is slowing: mean annual rate of population change was estimated to be 1.13 from 1980-89, 1.11 from 1990-1999 and 1.06 from 2000-2009. The fit to the Gulf region data is rather less impressive, and it is clear that there is something missing from the model to account for the unexplained variation in pup production estimates between closely spaced years. The estimated pup production appears relatively stable until around 1990, and has been gradually increasing thereafter. The fit to the Coastal Nova Scotia data is also less than satisfactory, with over-estimation at the beginning of the time period, although the fitted values are close to the data thereafter. One notable feature of the Coastal Nova Scotia estimates is the strong rise in pup production in 2003-2005. This corresponds with a very large pup harvest in this region in 2002, which is estimated to have just about wiped out the pup production for that year. This resulted in a strong movement response of females from other regions who are estimated to have colonized the region in 2002, recruited into the breeding population, and shown high breeding success from 2003 onwards. Although the estimated large increase in numbers seems implausible, it should be noted that it has almost no affect on the total pup production numbers, as numbers in the Coastal Nova Scotia region are very small compared with the other regions, particularly Sable Island.

Estimates of total population size at the beginning of each year (i.e., just after the breeding season, and so including pups, but before hunting or natural mortality) are shown by region in Figutr 4 and in Appendix Table A4. The trajectories generally mirror those of the pups. Estimated total population size in 2010, combined over all 3 regions is 348,900 (95%CI 291,300-414,900). This is 4% higher than the equivalent estimate for 2009 of 335,200 (95%CI 292,300-395,100) and 975% higher than the estimate for 1977 of 35,800 (95%CI 24,700-53,100). Estimates of overall mean annual population change were 1.06 from 1980-1989, 1.09 in 1990-1999, and 1.06 in 2000-2009.

We note in passing that estimates of population size in 2007 (302,200 with 95%CI 257,400-351,700) are very similar to those given by Thomas et al. (2007; 304,000 with 95% CI 242,000-371,000), which did not have the benefit of 2010 data, and used slightly different historical harvest figures. Confidence intervals are, however, narrower, as would be expected given the additional data.

Posterior parameter distributions are shown in Figure 5, together with the corresponding priors. The fecundity parameters (α_{max} and ρ) are almost identical to their priors, indicating that effectively nothing has been learnt about these from the pup production data over the

[1] Note that all results reported here on states are smoothed rather than filtered estimates, sensu e.g., Cappé et al. 2005. This just means that they are estimates computed using all the data, rather than just the data up to the time point for which the estimate is being made.

information specified in the prior distribution. Posterior maximum juvenile survival ($\phi_{p\max}$) is similar to the prior, although the mean is slightly higher. Posterior mean adult survival (ϕ_a) is also similar to the prior (0.96 vs 0.95 in the prior), but the posterior standard error is less than a third that of the prior, so the data have somewhat informative about this parameter. The posterior mean on the movement parameter γ is approximately half that specified by the prior (1.46 vs 2.5), and the standard error is much reduced, implying less movement than between regions anticipated, but still some. Note that this is in contrast to the analysis of Thomas et al. (2007) who found that movement was almost negligible. One difference in the current analysis is the high harvest numbers in Coastal Nova Scotia in 2002; the subsequent movement of recruiting females from other regions is consistent with the observed large increase in pup production there in following years. Estimated carrying capacity for Sable Island is much higher than the prior and greatly higher than current estimates of pup production, indicating little effect of density dependence as yet. By contrast, estimated carrying capacity for both the Gulf and Sable populations was close to the prior – although this is still far above current levels of pup production.

DISCUSSION

RELIABILITY OF RESULTS

Thomas et al. (2007) discuss three reasons why the results of their analysis may be treated with caution, and these reasons hold also for the analysis presented here.

Firstly, the model is clearly inadequate in some respects. It does not explain the large variation between closely-spaced surveys in observed pup production in the Gulf region. We therefore recommend viewing with caution the estimated pup production and total population size coming from this region. We discuss later possible extensions to address this. Our assumption that adult male and female survival is identical is questionable, given that males often have lower survival than females in body-size dimorphic species such as grey seals, as is the assumption that pregnancy rates and fecundity rates are equal among regions.

Secondly, being a Bayesian analysis, it is important to consider the sensitivity of the results to the priors. We anticipate high sensitivity of estimated parameter distributions in parameters where the posterior is very similar to the prior ($\alpha_{\max}$, ρ and $\phi_{p\max}$), and less for the other parameters. This sensitivity may affect the population size estimate somewhat – for example fecundity rate is closely related to population size since the number of breeding females is given by the estimated pup production divided by the fecundity rate. We anticipate that our priors on initial population sizes in 1977 will have little effect on estimates of current population size. These intuitions should, however, be tested.

Lastly, the fitting method may have influenced the result, although probably not to any significant extent. We do not think there is much Monte-Carlo error in our results. However, we achieved low MC error in part by trebling the observed SEs on pup production estimates, when evaluating the particle weights. The models should be re-run with the correct SEs – although it will take very significantly more particles to achieve the same reliability in the estimated posterior distributions. Our intuition is that this will have little effect on the posterior means, although it may reduce the SEs a little. We also made an arbitrary assumption to obtain SEs on total counts – although this probably had little effect on the inferences. The particle filtering algorithm included an auxiliary particle filter with kernel smoothing of parameters, and this is known to cause bias in theory, although Newman et al. (2009) found no discernable difference

between PF estimates and those from an MCMC sampler that was used as the "gold standard", with both simulated and real data applied to a seal model similar to the one used here. They used a kernel smoothing discount parameter of 0.997, while we used 0.9997, so we expect even less bias here – although the model and data are different so it is something worth investigating if possible. Attempting very large runs with no kernel smoothing is one possible way to attempt this.

A further issue, not discussed by Thomas et al. (2007) is the assumption of equal sex ratio among adult seals. It seems plausible that adult male survival is lower than that of adult females; indeed the UK grey seal population assessments assume a ratio of 0.73 males to each female, and there is recent evidence that this number may be even lower (Thomas 2010). Lowering the ratio would lower the population size estimate, although not in an entirely straightforward manner because the historical harvest estimates were pro-rated according to sex ratio, so a fresh run of the fitting algorithm would be required to obtain exact inference with a new sex ratio. However, to enable speedy calculation of approximate population size under different sex ratios, the estimated adult female population is given in Appendix Table A5. For example, to estimate population size for a ratio of 0.73 males per female, one would multiply the numbers in Appendix Table A5 by 1.73, and add the estimated pup production from Appendix Table A3.

Inferences about grey seal population dynamics

We found that the model used here does not show much evidence of a recent density-dependent slow-down in population growth, when calibrated with the pup production data. Our posterior estimates of carrying capacity are 3-20 times higher than current estimated levels of pup production; hence if the model is correct then in the absence of changes in management practices, seal populations will continue to rise at similar rates to those seen in the recent past. There are several reasons why this inference may be incorrect. Some were discussed in the previous section. In addition, carrying capacity is notoriously difficult to estimate from populations still growing rapidly. There is also every reason to expect that changing environmental conditions, or other limitations such as food stocks, may place a limit on seal numbers long before our estimated carrying capacities are reached.

We also found that allowing some degree of movement between colonies was helpful in achieving a reasonable fit of to data. This is something that bears further investigation.

The analysis of shot adult female seals performed by Thomas et al. (2007) showed no convincing evidence for a decline in age-specific pregnancy rates. By contrast, data from resightings of branded (marked) animals on Sable Island have shown an increase in mean age at first birth (Bowen et al. 2007). This suggests that density dependent factors may be beginning to operate in this segment of the population, and therefore that different factors may be operating in the different regions. Life history information has been collected from animals since 1983. Analyses of these data would provide insights into mortality patterns among mature and possibly juvenile animals hauling out on Sable Island. Recently, ultra-sound has been found to be an effective tool to determine if a female grey seal is pregnant (W.D. Bowen DFO, Dartmouth, NS, unpublished data). Increased sampling would provide information on late-term pregnancy rates for this colony which are also needed. It would be useful to include the Sable Island marked animal data in future analyses of population dynamics.

Future work

There are several directions in which this work could be extended. As mentioned above, the prior sensitivity needs investigating as does any bias caused by the fitting algorithm. There is a

clear need to extend the biological model to better match conditions in the Gulf region. Both pre- and post-weaning pup mortality in the Gulf is strongly decreased under a combination of poor ice conditions and storms, and it would be very useful to be able to introduce a covariate to account for this. Work is proceeding along these lines. In addition, it is likely that maximum pup survival is lower in the Gulf than the other regions. Other biological models could be considered, and model selection methods used to evaluate support for each. However, as with British Grey Seals, it is likely that there is little information in the data to distinguish between various plausible models without independent estimates of total population size (Thomas 2010). Nevertheless, unlike for British seals, the presence of a time series of information on pregnancy rates means that alternative plausible models are unlikely to predict extremely different total population sizes. Including additional information on survival, particularly adult male survival, would help considerably to improve the reliability of the modelling process.

Estimates of pup production and of harvest are available from 1960 onwards, so inference could start from this time, rather than 1977. Although this is unlikely to provide improved estimates of population size in recent times, it may be helpful to have the additional estimates of historical population size, for example to aid understanding of the interaction between seals and their prey species.

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Table 1. Prior parameter distributions for the state-space model of grey seal population dynamics.

Param	***Distribution***	***Mean***	***Stdev***
ϕ_a	Be(27.25,1.43)	0.95	0.04
$\phi_{p\max}$	Be(14.00,6.00)	0.7	0.1
χ_1	Ga(4,25000)	100000	50000
χ_2	Ga(4, 7500)	30000	15000
χ_3	Ga(4,1500)	6000	3000
$\alpha_{\max}$	Be(427.50,60.59)	0.876	0.015
ρ	Ga(64.29, 3.61×10^{-2})	2.319	0.29
γ	Ga(1.00,2.5)	2.5	2.5

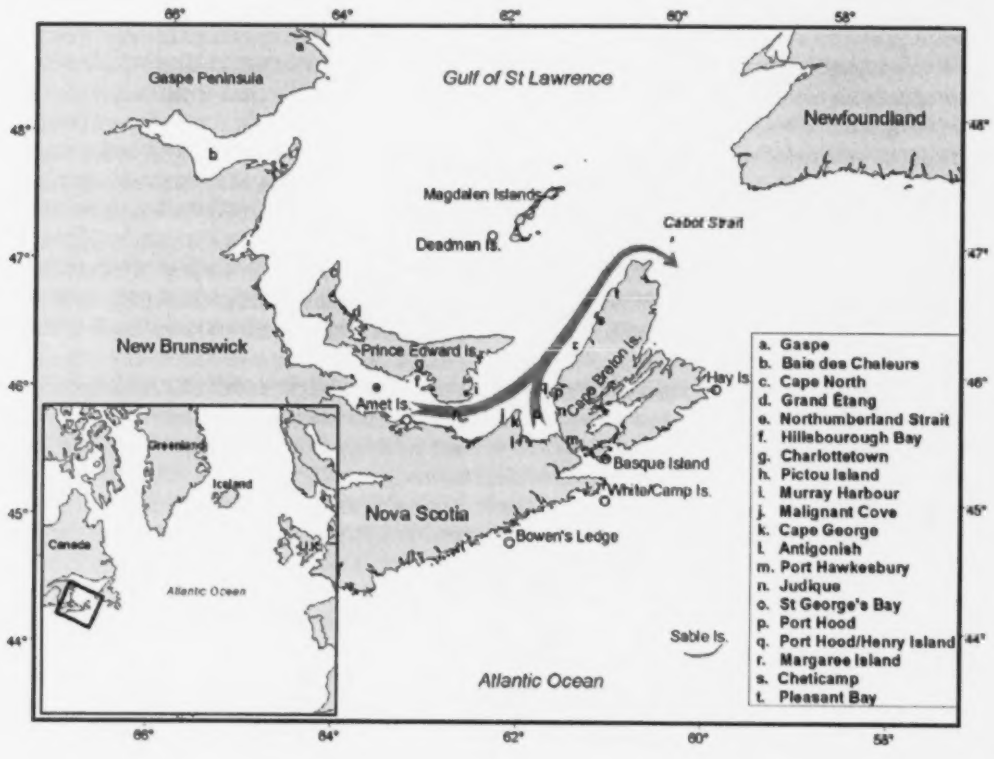

Figure 1. Area of interest in Eastern Canada showing locations where grey seal colonies can be found. The arrow represents the general direction of ice drift for pups born on the pack ice in Northumberland Strait.

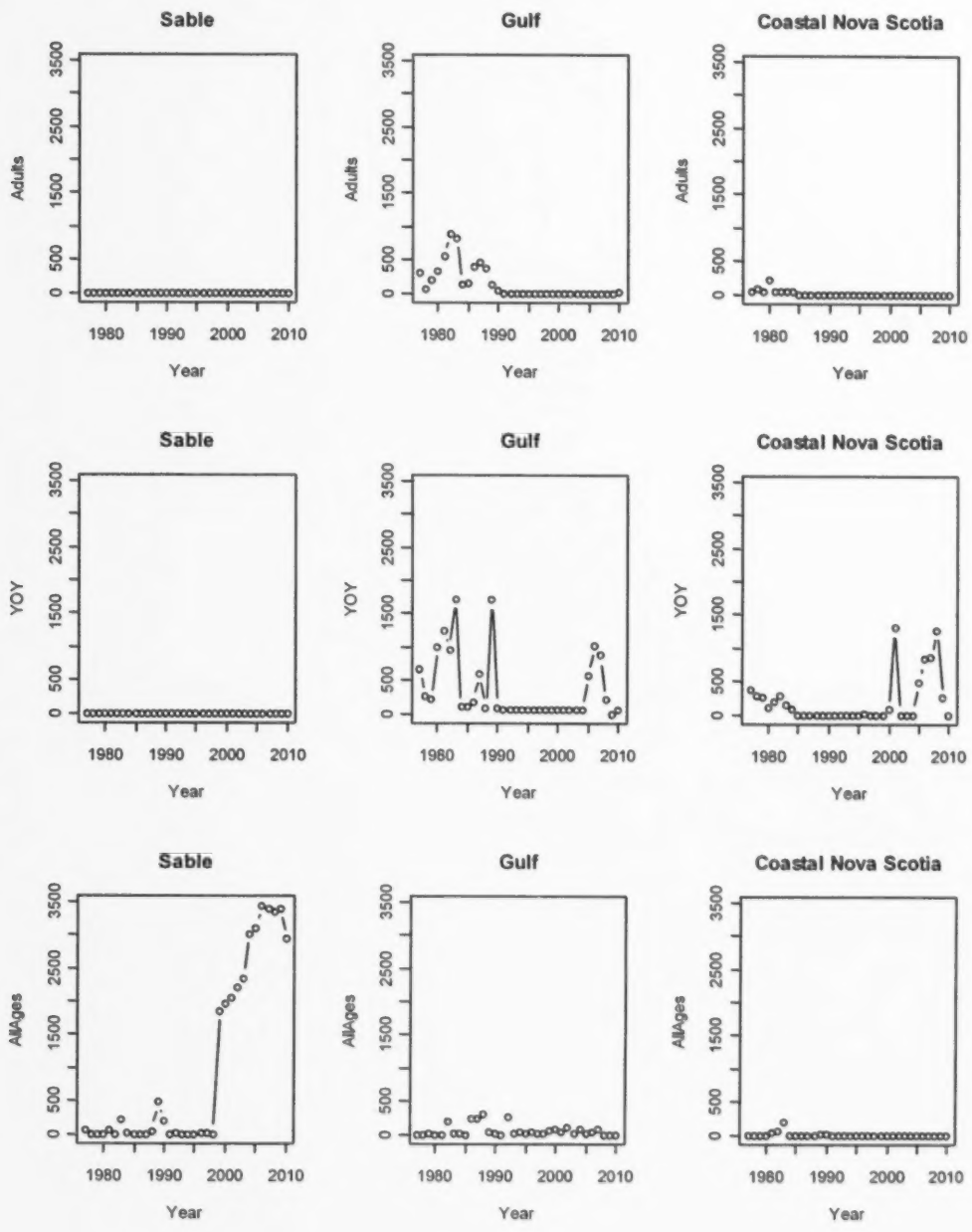

Figure 2. Number of seals harvested by commercial hunt and cull (first two rows, split into adults (ages 1+) and young-of-the-year (age 0)), and removal of nuisance animals and scientific sampling (bottom row). See also Appendix Table A2.

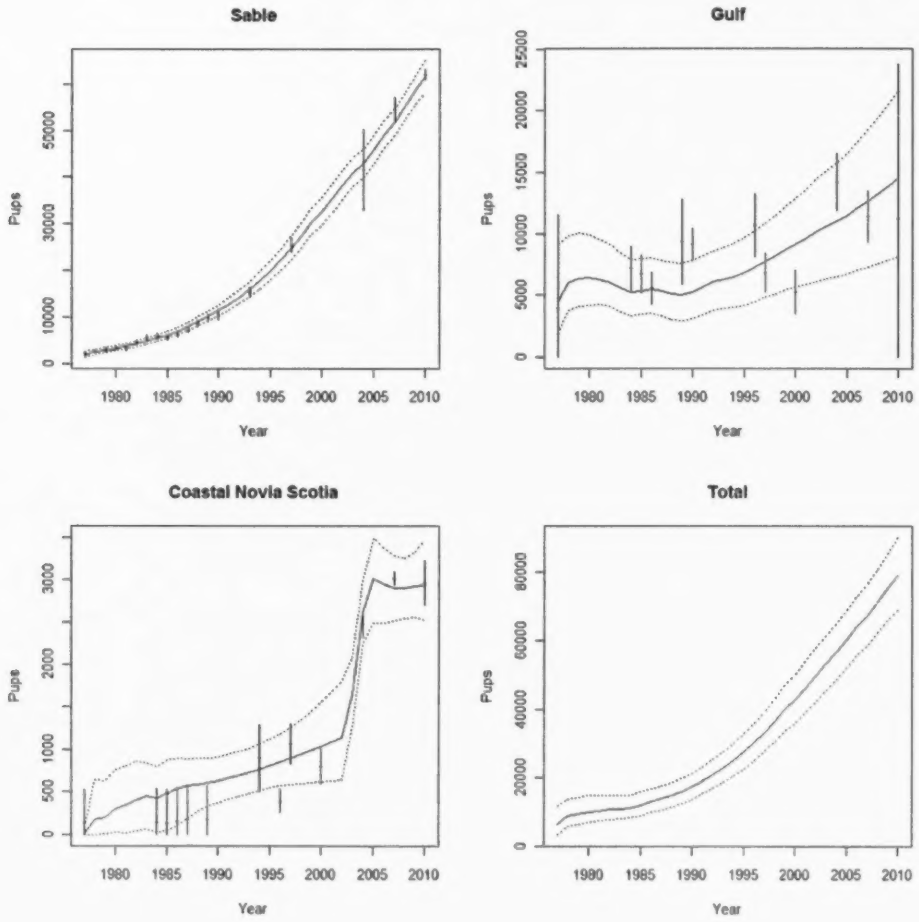

Figure 3. Estimates of true pup production from a model of grey seal population dynamics fit to pup production estimates from 1977-2010 in three regions. The smooth lines show the posterior mean bracketed by the 95% posterior credibility interval. The filled circles show estimated pup production from survey data and the vertical lines denote +/- 2 standard errors on these estimates (truncated at 0 where necessary).

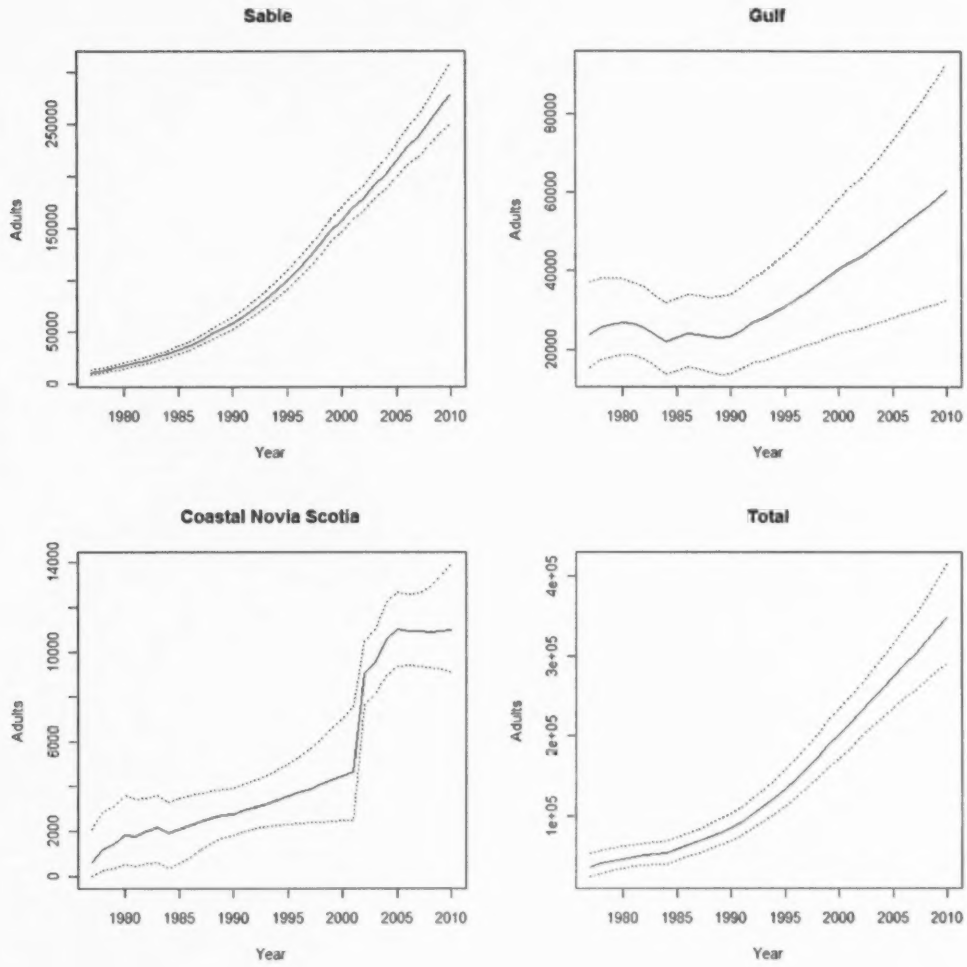

Figure 4. Estimates of total population size (including pups) from a model of grey seal population dynamics fit to pup production estimates from 1977-2010 in three regions. The smooth lines show the posterior mean bracketed by the 95% posterior credibility interval.

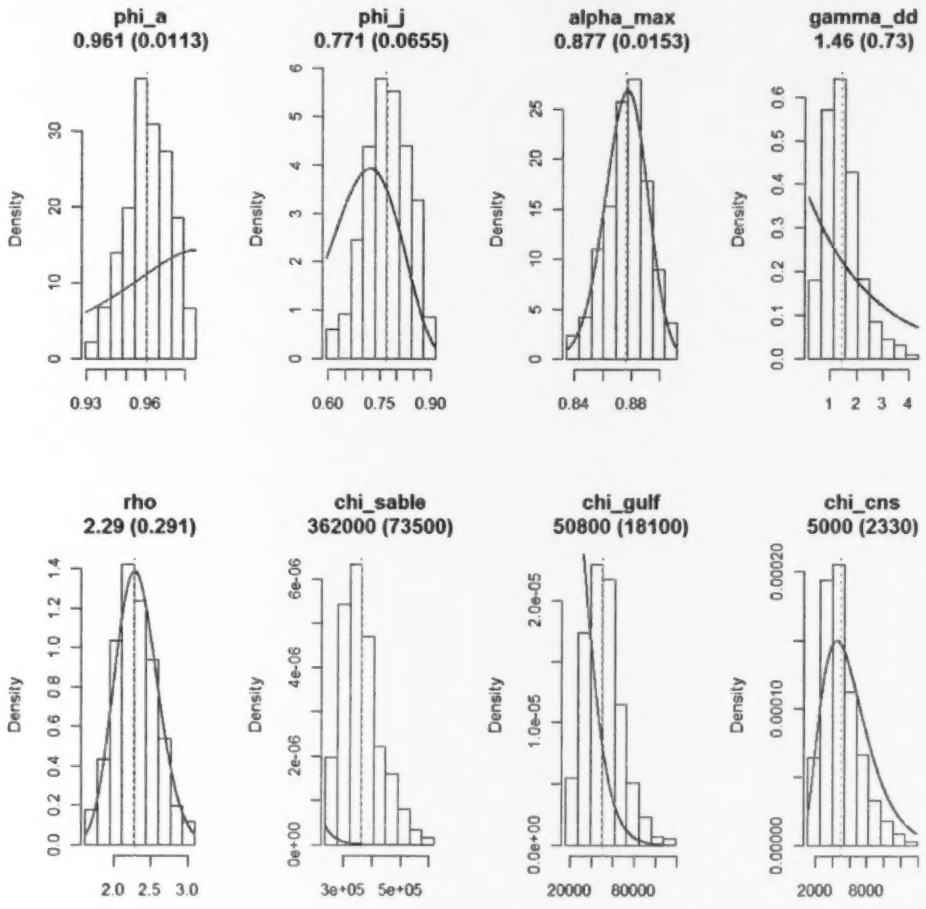

Figure 5. Posterior parameter estimates (histograms) and priors (solid lines) a model of grey seal population dynamics fit to pup production estimates from 1977-2010. The vertical line shows the posterior mean; its value (and standard error) is given in the title of each plot after the parameter name.

Appendix Table A1. Pup production data and associated SEs used in the state-space model analysis. Zero values indicate missing data. No data was available for Coastal Nova Scotia in 1977, so the values for 1976 (shown in italics) were used to form priors on pup production in the first year of the model.

Year	***Sable Island***		***Gulf***		***Coastal Nova Scotia***	
	Estimate	SE	Estimate	SE	Estimate	SE
1977	2181	173	3900	3900	*130*	*200*
1978	2687	192	0	0	0	0
1979	2933	201	0	0	0	0
1980	3344	214	0	0	0	0
1981	3143	208	0	0	0	0
1982	4489	248	0	0	0	0
1983	5435	273	0	0	0	0
1984	5856	283	7169	911	142	200
1985	5606	277	6706	795	135	200
1986	6301	294	5588	679	151	200
1987	7391	318	0	0	179	200
1988	8593	343	0	0	0	0
1989	9712	365	9352	1756	179	200
1990	10451	575	9176	649	0	0
1991	0	0	0	0	0	0
1992	0	0	0	0	0	0
1993	15500	463	0	0	0	0
1994	0	0	0	0	900	0
1995	0	0	0	0	0	0
1996	0	0	10717	1306	395	74
1997	25400	750	6839	800	1061	121
1998	0	0	0	0	0	0
1999	0	0	0	0	0	0
2000	0	0	5260	910	799	105
2001	0	0	0	0	0	0
2002	0	0	0	0	0	0
2003	0	0	0	0	0	0
2004	41500	4381	14210	1200	2469	76
2005	0	0	0	0	0	0
2006	0	0	0	0	0	0
2007	54482	1288	11413	1077	3017	40
2008	0	0	0	0	0	0
2009	0	0	0	0	0	0
2010	62054	587	11228	6442	2960	136

Appendix Table A2. Harvest data used in the state-space model analysis. Age and region categories not shown are all zero. Adults and YOY (young-of-the-year) refer to commercial harvest and cull data; AllAges refers to nuisance removals and scientific sampling.

Year	***Sable***	***Gulf***			***Coastal Nova Scotia***		
	AllAges	Adults	YOY	AllAges	Adults	YOY	AllAges
1977	69	308	673	0	34	373	0
1978	0	57	267	0	90	290	0
1979	0	190	215	9	45	269	0
1980	0	336	994	0	211	115	0
1981	69	552	1242	0	35	197	46
1982	0	880	961	199	42	276	69
1983	214	814	1721	12	45	152	197
1984	20	135	96	12	34	80	0
1985	0	141	113	0	0	0	0
1986	0	402	180	230	0	0	0
1987	0	456	593	249	0	0	0
1988	46	379	90	298	0	0	0
1989	477	138	1700	45	0	0	24
1990	197	48	88	16	0	0	9
1991	0	0	50	0	0	0	0
1992	6	0	50	260	0	0	0
1993	0	0	50	6	0	0	0
1994	0	0	50	39	0	0	0
1995	0	0	50	5	0	0	0
1996	24	0	50	33	0	6	0
1997	7	0	50	25	0	0	0
1998	0	0	50	20	0	0	0
1999	1849	0	50	69	0	0	0
2000	1967	0	50	89	0	82	0
2001	2054	0	50	39	0	1301	0
2002	2204	0	50	100	0	0	0
2003	2346	0	50	13	0	0	0
2004	3002	0	50	93	0	0	0
2005	3105	0	579	12	0	494	0
2006	3437	0	1027	28	0	830	0
2007	3373	0	879	87	0	868	0
2008	3334	0	210	0	0	1261	0
2009	3381	0	0	0	0	263	0
2010	2933	25	58	0	0	0	0

Appendix Table A3. Posterior estimates of pup production with 95% symmetric Bayesian Credibility Intervals (CIs).

Year	Sable Island	Gulf	Coastal Nova Scotia	Total
1977	1.9 (1.4 2.5)	4.5 (1.9 9.2)	0 (0 0.1)	6.4 (3.3 11.7)
1978	2.5 (2 3.1)	6.1 (3.8 9.8)	0.2 (0 0.6)	8.8 (5.8 13.5)
1979	2.9 (2.4 3.5)	6.4 (4.1 10.1)	0.2 (0 0.6)	9.4 (6.4 14.2)
1980	3.3 (2.8 3.9)	6.4 (4.2 10)	0.3 (0 0.8)	10 (7 14.6)
1981	3.8 (3.2 4.3)	6.3 (4.2 9.6)	0.3 (0 0.8)	10.4 (7.5 14.7)
1982	4.2 (3.7 4.8)	6 (4.1 9.1)	0.4 (0 0.9)	10.7 (7.8 14.8)
1983	4.8 (4.3 5.4)	5.6 (3.6 8.5)	0.4 (0.1 0.8)	10.9 (8 14.7)
1984	5.4 (4.8 6.1)	5.3 (3.4 7.9)	0.4 (0 0.8)	11.1 (8.2 14.8)
1985	6.1 (5.5 6.9)	5.4 (3.4 8)	0.5 (0 0.9)	12 (9 15.7)
1986	7 (6.2 7.7)	5.5 (3.5 8.1)	0.5 (0.1 0.9)	13 (9.9 16.7)
1987	7.9 (7.1 8.8)	5.3 (3.3 7.9)	0.6 (0.2 0.9)	13.8 (10.6 17.5)
1988	9 (8.1 9.9)	5.1 (3 7.6)	0.6 (0.3 0.9)	14.7 (11.4 18.4)
1989	10.2 (9.2 11.2)	5 (2.9 7.6)	0.6 (0.3 0.9)	15.8 (12.4 19.7)
1990	11.3 (10.2 12.5)	5.3 (3.1 7.8)	0.6 (0.4 0.9)	17.2 (13.6 21.2)
1991	12.7 (11.4 14)	5.6 (3.4 8.2)	0.7 (0.4 0.9)	19 (15.2 23.2)
1992	14.2 (12.7 15.7)	6.1 (3.8 8.6)	0.7 (0.4 1)	20.9 (17 25.3)
1993	15.9 (14.3 17.6)	6.3 (3.9 8.9)	0.7 (0.5 1)	22.9 (18.7 27.5)
1994	17.8 (16 19.7)	6.5 (4 9.2)	0.8 (0.5 1.1)	25 (20.5 30)
1995	19.9 (17.9 22.1)	6.8 (4.2 9.7)	0.8 (0.5 1.1)	27.5 (22.6 32.8)
1996	22.2 (20 24.6)	7.3 (4.5 10.2)	0.9 (0.6 1.2)	30.3 (25.1 36)
1997	24.7 (22.3 27.3)	7.7 (4.8 10.8)	0.9 (0.6 1.3)	33.3 (27.7 39.4)
1998	27.4 (24.8 30.2)	8.2 (5.1 11.5)	0.9 (0.6 1.3)	36.5 (30.6 43)
1999	30.3 (27.6 33.2)	8.7 (5.4 12.2)	1 (0.6 1.4)	40 (33.6 46.9)
2000	32.6 (29.7 35.6)	9.2 (5.6 12.9)	1 (0.6 1.5)	42.7 (36 50)
2001	35.3 (32.4 38.5)	9.6 (5.9 13.6)	1.1 (0.6 1.7)	46.1 (38.9 53.8)
2002	38.3 (35.3 41.5)	10.2 (6.1 14.4)	1.1 (0.6 1.8)	49.6 (42 57.7)
2003	41 (37.9 44.2)	10.6 (6.3 15.1)	1.7 (1.3 2.1)	53.2 (45.5 61.3)
2004	42.9 (39.9 46)	11 (6.5 15.7)	2.6 (2.2 3)	56.5 (48.7 64.7)
2005	45.8 (42.8 48.9)	11.5 (6.7 16.5)	3 (2.5 3.5)	60.3 (52 68.9)
2006	49.1 (46.2 52.1)	12.1 (7 17.5)	2.9 (2.5 3.4)	64.2 (55.7 73)
2007	51.8 (48.9 54.7)	12.7 (7.3 18.5)	2.9 (2.5 3.3)	67.3 (58.7 76.4)
2008	55.2 (52.3 58.2)	13.3 (7.6 19.5)	2.9 (2.5 3.2)	71.4 (62.4 80.9)
2009	58.7 (55.6 61.9)	13.9 (7.9 20.6)	2.9 (2.5 3.3)	75.6 (66.1 85.8)
2010	61.6 (58.2 65)	14.5 (8.2 21.6)	2.9 (2.5 3.5)	79 (68.9 90.1)

Appendix Table A4. Posterior estimates of total population size at the end of each breeding season (i.e., including pups), with 95% symmetric Bayesian Credibility Intervals (CIs).

Year	Sable Island	Gulf	Coastal Nova Scotia	Total
1977	11.3 (9.3 13.8)	23.9 (15.5 37.2)	0.6 (0 2.1)	35.8 (24.7 53.1)
1978	13.2 (11.1 15.8)	25.6 (17.3 38.2)	1.2 (0.2 2.9)	40 (28.7 56.9)
1979	15.3 (13 18)	26.4 (18.3 38.2)	1.4 (0.3 3.1)	43.1 (31.6 59.4)
1980	17.5 (15 20.5)	26.8 (18.8 38)	1.8 (0.5 3.6)	46.2 (34.4 62.1)
1981	20.1 (17.5 23.2)	26.5 (18.7 37.1)	1.8 (0.4 3.4)	48.4 (36.6 63.8)
1982	22.8 (19.9 26)	25.6 (17.8 36)	2 (0.6 3.5)	50.4 (38.3 65.4)
1983	25.8 (22.7 29.3)	23.7 (15.9 33.7)	2.2 (0.6 3.6)	51.7 (39.2 66.6)
1984	28.7 (25.4 32.4)	22 (13.8 32.1)	1.9 (0.3 3.3)	52.6 (39.5 67.8)
1985	32.6 (28.9 36.6)	23 (14.7 32.9)	2.1 (0.5 3.5)	57.6 (44.1 72.9)
1986	36.8 (32.9 41.1)	24.1 (15.7 34)	2.3 (0.8 3.6)	63.2 (49.3 78.8)
1987	41.7 (37.4 46.5)	23.9 (15.2 33.7)	2.5 (1.2 3.7)	68.1 (53.7 83.9)
1988	47.1 (42.4 52.3)	23.3 (14.3 33.4)	2.6 (1.5 3.8)	73 (58.1 89.5)
1989	53 (47.8 58.7)	23.1 (13.7 33.4)	2.7 (1.7 3.9)	78.8 (63.2 96)
1990	58.1 (52.4 64.3)	23.4 (13.9 33.9)	2.8 (1.8 3.9)	84.2 (68.1 102.2)
1991	65 (58.8 71.8)	24.9 (15.1 35.7)	2.9 (2 4.1)	92.8 (75.8 111.5)
1992	72.4 (65.7 79.9)	26.8 (16.6 38)	3.1 (2.1 4.3)	102.3 (84.4 122.1)
1993	80.8 (73.5 88.9)	27.9 (17.2 39.6)	3.2 (2.2 4.5)	111.9 (92.9 133)
1994	89.9 (82 98.6)	29.4 (18.2 41.9)	3.4 (2.3 4.7)	122.7 (102.4 145.3)
1995	99.8 (91.3 109.1)	31 (19.2 44.2)	3.6 (2.3 5)	134.3 (112.8 158.4)
1996	110.4 (101.4 120.3)	32.8 (20.2 46.8)	3.7 (2.4 5.3)	146.9 (123.9 172.4)
1997	121.8 (112.2 132.2)	34.5 (21.1 49.5)	3.9 (2.4 5.7)	160.2 (135.7 187.4)
1998	133.9 (123.8 144.8)	36.5 (22.1 52.3)	4.1 (2.4 6.1)	174.5 (148.3 203.3)
1999	146.9 (136.3 158.2)	38.4 (23.1 55.2)	4.3 (2.4 6.6)	189.5 (161.8 220)
2000	156.7 (145.6 168.6)	40.3 (24 58.1)	4.5 (2.5 7)	201.4 (172.1 233.7)
2001	168.8 (157.2 181.3)	42.2 (24.9 61.2)	4.7 (2.5 7.5)	215.7 (184.6 250)
2002	177.8 (165.9 190.3)	43.5 (25.4 63.2)	9 (7.7 10.5)	230.3 (199 264)
2003	190.6 (177.8 204.2)	45.5 (26.3 66.4)	9.5 (8.1 11)	245.7 (212.2 281.7)
2004	201 (187 215.9)	47.5 (27.2 69.7)	10.6 (9 12.2)	259.1 (223.2 297.9)
2005	213.9 (198.5 230.4)	49.5 (28.1 73.2)	11 (9.4 12.7)	274.5 (235.9 316.3)
2006	227.5 (210.2 246)	51.7 (29.1 77.1)	10.9 (9.4 12.6)	290.2 (248.7 335.6)
2007	237.5 (218.1 258.4)	53.8 (29.9 80.7)	10.9 (9.4 12.6)	302.2 (257.4 351.7)
2008	251.6 (229.6 275.3)	55.9 (30.8 84.6)	10.9 (9.3 12.9)	318.4 (269.8 372.8)
2009	266 (241.3 293)	58.2 (31.8 88.7)	10.9 (9.2 13.4)	335.2 (282.3 395.1)
2010	277.4 (249.6 308.3)	60.5 (32.7 92.8)	11 (9.1 13.9)	348.9 (291.3 414.9)

Appendix Table A5. Posterior estimates of total adult female population size (i.e., age 1 and older females), with 95% symmetric Bayesian Credibility Intervals (CIs). Estimated total population size (Appendix Table A4) is twice the adult female population size plus the pup production (Appendix Table A3).

Year	*Sable Island*	*Gulf*	*Coastal Nova Scotia*	*Total*
1977	4.7 (3.8 5.8)	9.7 (6.5 14.4)	0.3 (0 1)	14.7 (10.3 21.2)
1978	5.4 (4.5 6.4)	9.8 (6.7 14.2)	0.5 (0.1 1.1)	15.6 (11.3 21.8)
1979	6.2 (5.2 7.3)	10 (7.1 14.3)	0.6 (0.2 1.3)	16.8 (12.5 22.9)
1980	7.1 (6.1 8.3)	10.2 (7.3 14.2)	0.8 (0.3 1.4)	18.1 (13.6 24)
1981	8.2 (7.1 9.5)	10.1 (7.2 14)	0.7 (0.2 1.3)	19 (14.5 24.8)
1982	9.3 (8.1 10.7)	9.8 (6.8 13.6)	0.8 (0.3 1.3)	19.9 (15.2 25.6)
1983	10.5 (9.2 12)	9.1 (6.1 12.8)	0.9 (0.3 1.4)	20.4 (15.6 26.2)
1984	11.6 (10.2 13.2)	8.4 (5.2 12.2)	0.7 (0.1 1.3)	20.8 (15.6 26.7)
1985	13.2 (11.7 14.9)	8.8 (5.6 12.6)	0.8 (0.2 1.3)	22.8 (17.5 28.9)
1986	14.9 (13.3 16.8)	9.3 (6 13)	0.9 (0.4 1.4)	25.1 (19.6 31.2)
1987	16.9 (15.1 19)	9.3 (5.9 13)	0.9 (0.5 1.4)	27.1 (21.5 33.4)
1988	19.1 (17 21.3)	9.1 (5.6 12.9)	1 (0.6 1.5)	29.1 (23.2 35.7)
1989	21.4 (19.2 23.9)	9 (5.4 13)	1.1 (0.7 1.5)	31.5 (25.2 38.4)
1990	23.4 (21 26)	9 (5.4 13.1)	1.1 (0.7 1.5)	33.5 (27.1 40.7)
1991	26.2 (23.5 29.1)	9.6 (5.8 13.9)	1.1 (0.8 1.6)	36.9 (30.1 44.5)
1992	29.1 (26.3 32.3)	10.3 (6.4 14.8)	1.2 (0.8 1.7)	40.7 (33.5 48.8)
1993	32.5 (29.4 35.9)	10.8 (6.6 15.5)	1.3 (0.8 1.7)	44.5 (36.8 53.2)
1994	36.1 (32.7 39.8)	11.4 (7 16.5)	1.3 (0.9 1.8)	48.8 (40.6 58.1)
1995	40 (36.4 43.9)	12.1 (7.4 17.4)	1.4 (0.9 2)	53.4 (44.7 63.3)
1996	44.1 (40.3 48.3)	12.7 (7.8 18.4)	1.4 (0.9 2.1)	58.3 (48.9 68.8)
1997	48.5 (44.5 53)	13.4 (8.1 19.4)	1.5 (0.9 2.2)	63.5 (53.5 74.6)
1998	53.3 (49 58)	14.1 (8.5 20.4)	1.6 (0.9 2.4)	69 (58.3 80.8)
1999	58.3 (53.7 63.3)	14.9 (8.8 21.6)	1.6 (0.9 2.6)	74.8 (63.4 87.4)
2000	62.1 (57.2 67.4)	15.6 (9.1 22.6)	1.7 (0.9 2.8)	79.3 (67.2 92.8)
2001	66.7 (61.4 72.4)	16.3 (9.4 23.8)	1.8 (0.9 2.9)	84.8 (71.8 99.2)
2002	69.7 (64.2 75.6)	16.7 (9.6 24.5)	3.9 (3.2 4.7)	90.4 (77 104.9)
2003	74.8 (68.7 81.4)	17.5 (9.9 25.8)	3.9 (3.3 4.6)	96.2 (81.9 111.8)
2004	79.1 (72.3 86.3)	18.2 (10.3 27.1)	4 (3.3 4.6)	101.3 (85.9 118.1)
2005	84.1 (76.6 92.2)	19 (10.6 28.5)	4 (3.4 4.7)	107.1 (90.5 125.4)
2006	89.2 (80.8 98.3)	19.8 (11 30)	4 (3.4 4.7)	113 (95.2 132.9)
2007	92.9 (83.6 103.1)	20.6 (11.3 31.3)	4 (3.4 4.8)	117.4 (98.2 139.1)
2008	98.2 (87.8 109.6)	21.3 (11.6 32.7)	4 (3.3 4.9)	123.5 (102.7 147.3)
2009	103.6 (92 116.5)	22.2 (11.9 34.3)	4 (3.3 5.1)	129.8 (107.2 155.9)
2010	107.9 (95 122.5)	23 (12.2 35.8)	4 (3.2 5.2)	135 (110.5 163.5)